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PROGRESSIVE EVOLUTION AND THE ORIGIN OF SPECIES¹

PROFESSOR ARTHUR DENDY

THE opening years of the present century have witnessed a remarkable development of biology as an experimental science, a development which, however full of promise it may be for the future, for the time being appears to have resulted in a widespread disturbance of ideas which have themselves only recently succeeded in gaining general acceptance. The theory of organic evolution, plainly enough enunciated at the close of the eighteenth and the beginning of the nineteenth century by Buffon, Lamarck, and Erasmus Darwin, remained unconvincing to the great majority of thinking men until the genius of Charles Darwin not only brought together and presented the evidence in such a manner that it could no longer be ignored, but elaborated a logical explanation of the way in which organic evolution might be supposed to have taken place. Thanks to his labors and those of Alfred Russel Wallace, supported by the powerful influence of such men as Huxley and Hooker, the theory was placed upon a firm foundation, in a position which can never again be assailed with any prospect of success.

This statement is, I believe, entirely justified with regard to the theory of organic evolution itself, but the case is very different when we come to investigate the position of the various subsidiary theories which have been put forward from time to time with regard to what may perhaps be termed the *modus operandi*, the means by which organic evolution has been effected. It is in this field that controversy rages more keenly than ever before. Lamarck told us that evolution was due to the

¹ Address of the president of the section of zoology, British Association for the Advancement of Science, Australia, 1914.

accumulated results of individual effort in response to a changing environment, and also to the direct action of the environment upon the organism. Darwin and Wallace taught us that species originated by the natural selection of favorable variations, and under the influence of Weismann's doctrine of the non-inheritance of acquired characters the theory of natural selection is in danger of becoming crystallized into an inflexible dogma. In recent years de Vries has told us that species arise by sudden mutations, and not by slow successive changes, while one of the most extreme exponents of "Mendelism," Professor Lotsy, lately informed us that all species arise by crossing, and seriously suggested that the vertebrate type arose by the crossing of two invertebrates!

This curious and many-sided divergence of opinion amongst expert biologists is undoubtedly largely due to the introduction of experimental methods into biological science. Such methods have proved very fruitful in results which at first sight seem to be mutually contradictory, and each group of workers has built up its own theory mainly on the basis of observations in its own restricted field.

Professor Bateson has said in his recently published "Problems of Genetics":

When . . . we contemplate the problem of evolution at large the hope at the present time of constructing even a mental picture of that process grows weak almost to the point of vanishing. We are left wondering that so lately men in general, whether scientific or lay, were so easily satisfied. Our satisfaction, as we now see, was chiefly founded on ignorance.²

In view of this striking pronouncement on the part of one who has devoted his life with signal success to the experimental investigation of evolutionary problems, the remarks which I propose to lay before you for your consideration to-day may well appear rash and ill-advised. I cannot believe, however, that the position is really quite so black as it is painted. We must perforce admit that the divers theories with regard to the work-

² "Problems of Genetic," p. 97.

ing of organic evolution cannot all be correct in all their details, but it may be that each contains its own elements of truth, and that if these elements can but be recognized and sorted out, they may perhaps be recombined in such a form as to afford at any rate a plausible working hypothesis. We must bear in mind from the outset that in dealing with such a complex problem many factors have to be taken into account, and that widely different views on the question may be merely one-sided and not necessarily mutually exclusive.

I take it there are three principal facts, or groups of facts, that have to be accounted for by any theory of organic evolution:

1. The fact that, on the whole, evolution has taken place in a progressive manner along definite and divergent lines.

2. The fact that individual animals and plants are more or less precisely adapted in their organization and in their behavior to the conditions under which they have to live.

3. The fact that evolution has resulted in the existence on the earth to-day of a vast number of more or less well-defined groups of animals and plants which we call species.

The first of these facts appears to me to be the most fundamental, and at the same time the one to which least attention is usually paid. The great question, after all, is, Why do organisms progress at all instead of remaining stationary from generation to generation? To answer this question it is not necessary to go back to the beginning and consider the case of the first terrestrial organisms, whatever they may have been, nor are we obliged to take as illustrations the lowest organisms known to us as existing at the present day. We may consider the problem at any stage of evolution, for at each stage progress is, or may be, still taking place. We may even begin by considering what is usually regarded as the highest stage of all, man himself; and indeed this seems the most natural thing to do, for we

certainly know more about the conditions of progress in man than in any other organism. I refer, of course, at the moment, not to progress in bodily organization, but to progress in the ordinary sense of the word, the progress, say, of a family which rises in the course of a few generations from a position of obscure poverty to one of wealth and influence. You may perhaps say that such a case has no bearing upon the problem of organic evolution in a state of nature, and that we ought to confine our attention to the evolution of bodily structure and function. If so, I must reply that you have no right to limit the meaning of the term evolution in this manner; the contrast between man and nature is purely arbitrary; man is himself a living organism, and all the improvements that he effects in his own condition are part of the progress of evolution in his particular case. At any rate I must ask you to accept this case as our first illustration of a principle that may be applied to organisms in general.

If we inquire into the cause of the progress of our human family I think there can be only one answer—it is due to the accumulation of capital, or, as I should prefer to put it, to the accumulation of potential energy, either in the form of material wealth or of education. What one generation saves is available for the next, and thus each succeeding generation gets a better start in life, and is able to rise a little higher than the preceding one.

Every biologist knows, of course, that there are many analogous cases amongst the lower animals, and also amongst plants. The accumulation of food-yolk in the egg has undoubtedly been one of the chief factors in the progressive evolution of animals, although it has been replaced in the highest forms by a more effective method of supplying potential energy to the developing offspring. It may indeed be laid down as a general law that each generation, whether of animals or of plants, accumulates more energy than it requires for its own maintenance, and uses the surplus to give the next gen-

eration a start in life. There is every reason to believe that this has been a progressive process throughout the whole course of evolution, for the higher the degree or organization the more perfect do we find the arrangements for securing the welfare of the offspring.

We cannot, of course, trace this process back to its commencement, because we know nothing of the nature of the earliest living things, but we may pause for a moment to inquire whether any phenomena occur amongst simple unicellular organisms that throw any light upon the subject. What we want to know is—How did the habit of accumulating surplus energy and handing it on to the next generation first arise?

Students of Professor H. S. Jennings's admirable work on the "Behavior of the Lower Organisms" will remember that his experiments have led him to the conclusion that certain Protozoa, such as *Stentor*, are able to learn by experience how to make prompt and effective responses to certain stimuli; that after they have been stimulated in the same way a number of times they make the appropriate response at once without having to go through the whole process of trial and error by which it was first attained. In other words, they are able by practise to perform a given action with less expenditure of energy. Some modification of the protoplasm must take place which renders the performance of an act the easier the oftener it has been repeated. The same is, of course, true in the case of the higher animals, and we express the fact most simply by saying that the animal establishes habits. From the mechanistic point of view we might say that the use of the machine renders it more perfect and better adapted for its purpose. In the present state of our knowledge I think we cannot go beyond this, but must content ourselves with recognizing the power of profiting by experience as a fundamental property of living protoplasm.

It appears to me that this power of profiting by experience lies at the root of our problem, and that in it

we find a chief cause of progressive evolution. Jennings speaks of the principle involved here as the "Law of the readier resolution of physiological states after repetition," and, similarly, I think we must recognize a "Law of the accumulation of surplus energy" as resulting therefrom. Let us look at the case of the accumulation of food-yolk by the egg-cell a little more closely from this point of view. Every cell takes in a certain amount of potential energy in the form of food for its own use. If it leads an active life either as an independent organism or as a constituent part of an organism, it may expend by far the greater part, possibly even the whole, of that energy upon its own requirements, but usually something is left over to be handed down to its immediate descendants. If, on the other hand, the cell exhibits very little activity and expends very little energy, while placed in an environment in which food is abundant, it will tend to accumulate surplus energy in excess of its own needs. Such is the case with the egg-cells of the multicellular animals and plants. Moreover, the oftener the process of absorbing food-material is repeated the easier does it become; in fact, the egg-cell establishes a habit of storing up reserve material or food-yolk. Inasmuch as it is a blastogenic character, there can be no objection to the supposition that this habit will be inherited by future generations of egg-cells. Indeed we are obliged to assume that this will be the case, for we know that the protoplasm of each succeeding generation of egg-cells is directly continuous with that of the preceding generation. We thus get at any rate a possibility of the progressive accumulation of potential energy in the germ-cells of successive generations of multicellular organisms, and, of course, the same argument holds good with regard to successive generations of *Protista*.

It would seem that progressive evolution must follow as a necessary result of the law of the accumulation of surplus energy in all cases where there is nothing to

counteract that law, for each generation gets a better start than its predecessor, and is able to carry on a little further its struggle for existence with the environment. It may be said that this argument proves too much, that if it were correct all organisms would by this time have attained to a high degree of organization, and that at any rate we should not expect to find such simple organisms as bacteria and *Amebæ* still surviving. This objection, which, of course, applies equally to other theories of organic evolution, falls to the ground when we consider that there must be many factors of which we know nothing which may prevent the establishment of progressive habits and render impossible the accumulation of surplus energy. Many of the lower organisms, like many human beings, appear to have an inherent incapacity for progress, though it may be quite impossible for us to say to what that incapacity is due.

It will be observed that in the foregoing remarks I have concentrated attention upon the storing up of reserve material by the egg-cells, and in so doing have avoided the troublesome question of the inheritance of so-called acquired characters. I do not wish it to be supposed, however, that I regard this as the only direction in which the law of the accumulation of surplus energy can manifest itself, for I believe that the accumulation of surplus energy by the body may be quite as important as a factor in progressive evolution as the corresponding process in the germ-cells themselves. The parents, in the case of the higher animals, may supply surplus energy, in the form of nutriment or otherwise, to the offspring at all stages of its development, and the more capital the young animal receives the better will be its chances in life, and the better those of its own offspring.

In all these processes, no doubt, natural selection plays an important part, but, in dealing with the accumulation of food material by the egg-cells, one of my objects has been to show that progressive evolution would take place

even if there were no such thing as natural selection, that the slow successive variations in this case are not chance variations, but due to a fundamental property of living protoplasm and necessarily cumulative.

Moreover, the accumulation of surplus energy in the form of food-yolk is only one of many habits which the protoplasm of the germ-cells may acquire in a cumulative manner. It may learn by practise to respond with increased promptitude and precision to other stimuli besides that of the presence of nutrient material in its environment. It may learn to secrete a protective membrane, to respond in a particular manner to the presence of a germ-cell of the opposite sex, and to divide in a particular manner after fertilization has taken place.

Having thus endeavored to account for the fact that progressive evolution actually occurs by attributing it primarily to the power possessed by living protoplasm of learning by experience and thus establishing habits by which it is able to respond more quickly to environmental stimuli, we have next to inquire what it is that determines the definite lines along which progress manifests itself.

Let us select one of these lines and investigate it as fully as the time at our disposal will permit, with the view of seeing whether it is possible to formulate a reasonable hypothesis as to how evolution may have taken place. Let us take the line which we believe has led up to the evolution of air-breathing vertebrates. The only direct evidence at our disposal in such a case is, of course, the evidence of paleontology, but I am going to ask you to allow me to set this evidence, which, as you know, is of an extremely fragmentary character, aside, and base my remarks upon the ontogenetic evidence, which, although indirect, will, I think, be found sufficient for our purpose. One reason for concentrating our attention upon this aspect of the problem is that I wish to show that the recapitulation of phylogenetic history in individual development is a logical necessity if evolution has really taken place.

We may legitimately take the nucleated Protozoon cell as our starting point, for, whatever may have been the course of evolution that led up to the cell, there can be no question that all the higher organisms actually start life in this condition.

We suppose, then, that our ancestral Protozoon acquired the habit of taking in food material in excess of its own requirements, and of dividing into two parts whenever it reached a certain maximum size. Here again we must, for the sake of simplicity, ignore the facts that even a Protozoon is by no means a simple organism, and that its division, usually at any rate, is a very complicated process. Each of the daughter-cells presently separates from its sister-cell and goes its own way as a complete individual, still a Protozoon. It seems not improbable that the separation may be due to the renewed stimulus of hunger, impelling each cell to wander actively in search of food. In some cases, however, the daughter-cells remain together and form a colony, and probably this habit has been rendered possible by a sufficient accumulation of surplus energy in the form of food-yolk on the part of the parent rendering it unnecessary for the daughter-cells to separate in search of food at such an early date. One of the forms of colony met with amongst existing Protozoa is the hollow sphere, as we see it, for example, in *Sphærozoum* and *Volvox*, and it is highly probable that the assumption of this form is due largely, if not entirely, to what are commonly called mathematical causes, though we are not in a position to say exactly what these causes may be. The widespread occurrence of the blastosphere or blastula stage in ontogeny is a sufficiently clear indication that the hollow, spherical Protozoon colony formed a stage in the evolution of the higher animals.

By the time our ancestral organism has reached this stage, and possibly even before, a new complication has arisen. The cells of which the colony is composed no longer remain all alike, but become differentiated, pri-

marily into two groups, which we distinguish as somatic-cells and germ-cells respectively.

From this point onwards evolution ceases to be a really continuous process, but is broken up into a series of ontogenies, at the close of each of which the organism has to go back and make a fresh start in the unicellular condition, for the somatic cells sooner or later become exhausted in their conflict with the environment and perish, leaving the germ-cells behind to take up the running. That the germ-cells do not share the fate of the somatic cells must be attributed to the fact that they take no part in the struggle for existence to which the body is exposed. They simply multiply and absorb nutriment under the protection of the body, and therefore retain their potential energy unimpaired. They are in actual fact, as is so often said, equivalent to so many protozoa, and, like the protozoa, are endowed with a potential immortality.

We know that, if placed under suitable conditions, or in other words, if exposed to the proper environmental stimuli, these germ-cells will give rise to new organisms, like that in the body of which they were formerly enclosed. One of the necessary conditions is, with rare exceptions, the union of the germ-cells in pairs to form zygotes or fertilized ova; but I propose, in the first instance, for the sake of simplicity, to leave out of account the existence of the sexual process and the results that follow therefrom, postponing the consideration of these to a later stage of our inquiry. I wish, moreover, to make it quite clear that organic evolution must have taken place if no such event as amphimixis had ever occurred.

What, then, may the germ-cells be expected to do? How are they going to begin their development? In endeavoring to answer this question we must remember that the behavior of an organism at any moment depends upon two sets of factors—the nature of its own constitution on one hand, and the nature of its environ-

ment on the other. If these factors are identical for any two individual organisms, then the behavior of these two individuals must be the same. If the germ-cells of any generation are identical with those of the preceding generation, and if they develop under identical conditions, then the soma of the one generation must also be identical with that of the other.³ Inasmuch as they are parts of the same continuous germ-plasm—leaving out of account the complications introduced by amphimixis—we may assume that the germ-cells of the two generations are indeed identical in nearly every respect; but there will be a slight difference, due to the fact that those of the later generation will have inherited a rather larger supply of initial energy and a slightly greater facility for responding to stimuli of various kinds, for the gradual accumulation of these properties will have gone a stage further. The environment also will be very nearly identical in the two cases, for we know from experiment that if it were not the organism could not develop at all.

Throughout the whole course of its ontogeny the organism must repeat with approximate accuracy the stages passed through by its ancestors, because at every stage there will be an almost identical organism exposed to almost identical stimuli. We may, however, expect an acceleration of development and a slight additional progress at the end of ontogeny as the result of the operation of the law of the accumulation of surplus energy and of the slightly increased facility in responding to stimuli. The additional progress, of course, will probably be so slight that from one generation to the next we should be quite unable to detect it, and doubtless there will be frequent backslidings due to various causes.

We can thus formulate a perfectly reasonable explanation of how it is that the egg first undergoes segmentation and then gives rise to a blastula resembling a hol-

³ This is, of course, a familiar idea. Compare Driesch, "Gifford Lectures," 1907, p. 214.

low protozoon colony; it does so simply because at every stage it must do what its ancestors did under like conditions. We can also see that progressive evolution must follow from the gradual accumulation of additions at the end of each ontogeny, these additions being rendered possible by the better start which each individual gets at the commencement of its career.

Let us now glance for a moment at the next stage in phylogeny, the conversion of the hollow spherical protozoon colony into the cœlenterate type of organization, represented in ontogeny by the process of gastrulation. Here again it is probable that this process is explicable to a large extent upon mechanical principles. According to Rhumbler,⁴ the migration of endoderm cells into the interior of the blastula is partly due to chemotaxis and partly to changes of surface tension, which decreases on the inner side of the vegetative cells owing to chemical changes set up in the blastocœl fluid.

We may, at this point, profitably ask the question, Is the endoderm thus formed an inherited feature of the organism? The material of which it is composed is, of course, derived from the egg-cell continuously by repeated cell-division, but the way in which that material is used by the organism depends upon the environment, and we know from experiment that modifications of the environment actually do produce corresponding modifications in the arrangement of the material. We know, for example, that the addition of salts of lithium to the water in which certain embryos are developing causes the endoderm to be protruded instead of invaginated, so that we get a kind of inside-out gastrula, the well-known lithium larva.

It appears, then, that an organism really inherits from its parents two things: (1) a certain amount of protoplasm loaded with potential energy, with which to begin operations, and (2) an appropriate environment. Ob-

⁴ Quoted by Przibram, "Experimental Zoology," English Trans., Part I, p. 47.

vously the one is useless without the other. An egg can not develop unless it is provided with the proper environment at every stage. Therefore, when we say that an organism inherits a particular character from its parents, all we mean is that it inherits the power to produce that character under the influence of certain environmental stimuli.⁵ The inheritance of the environment is of at least as much importance as the inheritance of the material of which the organism is composed. The latter, indeed, is only inherited to a very small extent, for the amount of material in the egg-cell may be almost infinitesimal in comparison with the amount present in the adult, nearly the whole of which is captured from the environment and assimilated during ontogeny.

From this point of view the distinction between somatogenic and blastogenic characters really disappears, for all the characters of the adult organism are acquired afresh in each generation as a result of response to environmental stimuli during development. This is clearly indicated by the fact that you cannot change the stimuli without changing the result.

Time forbids us to discuss the phylogenetic stages through which the coelenterate passed into the coelomate type, the coelomate into the chordate, and the chordate into the primitive vertebrate. We must admit that as yet we know nothing of the particular causes that determined the actual course of evolution at each successive stage. What we do know, however, about the influence of the environment, both upon the developing embryo and upon the adult, is sufficient to justify us in believing that every successive modification must have been due to a response on the part of the organism to some environmental change. Even if the external conditions remained practically identical throughout long periods of time, we must remember that the internal conditions would be different in each generation, because

⁵ Compare Dr. Archdall Reid's suggestive essay on "Biological Terms" (*Bedrock*, January, 1914).

each generation starts with a slightly increased capital and carries on its development a little further under internal conditions modified accordingly.

At this point it may be asked, Is the response to environmental stimuli a purely mechanical one, and, if so, how can we account for the fact that at every stage in its evolution the organism is adapted to its environment? We shall have to return to this question later on, but it may be useful to point out once more that there is good reason to believe—especially from the experimental work of Jennings—that the response of even a unicellular organism to stimuli is to a large extent purposive; that the organism learns by experience, by a kind of process of trial and error, how to make the response most favorable to itself under any given change of conditions; in other words, that the organism selects those modes of response that are most conducive to its own well-being. Under the term response to stimuli we must, of course, include those responses of the living protoplasm which result in modifications of bodily structure, and hence the evolution of bodily structure will, on the whole, be of an adaptive character and will follow definite lines. There is good reason for believing, however, that many minor modifications in structure may arise and persist, incidentally as it were, that have no significance as adaptations.

One of the most remarkable and distinctive features of the lower vertebrates is the presence of gill-slits as accessory organs of respiration. These gill-slits are clearly an adaptation to aquatic life. When the ancestors of the higher vertebrates left the water and took to life on land the gills disappeared and were replaced by lungs, adapted for air-breathing. The change must, of course, have been an extremely gradual one, and we get a very clear indication of how it took place in the surviving dipnoids, which have remained in this respect in an intermediate condition between the fishes and the amphibia, possessing and using both gills and lungs.

We also know that even the most highly specialized air-breathing vertebrates, which never live in water and never require gills or gill-slits at all, nevertheless possess very distinct gill-slits during a certain period of their development. This is one of the most familiar illustrations of the law of recapitulation, and my only excuse for bringing it forward now is that I wish, before going further, to consider a difficulty—perhaps more apparent than real—that arises in connection with such cases.

It might be argued that if gill-slits arose in response to the stimuli of aquatic life, and if these stimuli are no longer operative in the case of air-breathing vertebrates, then gill-slits ought not to be developed at any stage of their existence. This argument is, I think, fully met by the following considerations.

At any given moment of ontogenetic development the condition of any organ is merely the last term of a series of morphogenetic stages, while its environment at the same moment—which, of course, includes its relation to all the other organs of the body—is likewise merely the last term of a series of environmental stages. We have thus two parallel series of events to take into consideration in endeavoring to account for the condition of any part of an organism—or of the organism as a whole—at any period of its existence:

E_1	E_2	E_3	...	E_n	environmental stages,
M_1	M_2	M_3	...	M_n	morphogenetic stages.

Ontogeny is absolutely conditioned by the proper correlation of the stages of these two series at every point, and hence it is that any sudden change of environment is usually attended by disastrous consequences. Thus, after the fish-like ancestors of air-breathing vertebrates had left the water and become amphibians, they doubtless still had to go back to the water to lay their eggs, in order that the eggs might have the proper conditions for their development.

Obviously the environment can only be altered with extreme slowness, and one of the first duties of the parent is to provide for the developing offspring conditions as nearly as possible identical with those under which its own development took place. It is, however, inevitable that, as phylogenetic evolution progresses, the conditions under which the young organism develops should change. In the first place, the mere tendency to acceleration of development, to which we have already referred, must tend to dislocate the correlation between the ontogenetic series and the environmental series. Something of this kind seems to have taken place in the life-cycle of many hydrozoa, resulting in the suppression of the free medusoid generation and the gradual degeneration of the gonophore. But it is probably in most cases change in the environment of the adult that is responsible for such dislocation.

To return to the case of the amphibians. At the present day some amphibians, such as the newts and frogs, still lay their eggs in water, while the closely related salamanders retain them in the oviducts until they have developed into highly organized aquatic larvæ, or even what is practically the adult condition. Kammerer has shown that the period at which the young are born can be varied by changing the environment of the parent. In the absence of water the normally aquatic larvæ of the spotted salamander may be retained in the oviduct until they have lost their gills, and they are then born in the fully-developed condition, while, conversely, the alpine salamander, of which the young are normally born in the fully-developed state, without gills, may be made to deposit them prematurely in water in the larval, gill-bearing condition.

There can be no doubt that the ancestral amphibians laid their eggs in water in a completely undeveloped condition. The habit of retaining them in the body during their development must have arisen very gradually in the phylogenetic history of the salamanders, the period

for which the young were retained growing gradually longer and longer. It is obvious that this change of habit involves a corresponding change in the environmental conditions under which the young develop, and in cases in which the young are not born until they have reached practically the adult condition this change directly affects practically the whole ontogeny. We may say that the series

$$\begin{array}{ccccccc} E_1 & E_2 & E_3 & \dots & E_n & \text{has become} \\ E_1' & E_2' & E_3' & \dots & E_n', \end{array}$$

and as the change of environment must produce its effect upon the developing organism the series

$$\begin{array}{ccccccc} M_1 & M_2 & M_3 & \dots & M_n & \text{will have become} \\ M_1' & M_2' & M_3' & \dots & M_n'. \end{array}$$

We must remember that throughout the whole course of phylogenetic evolution this series is constantly lengthening, so that what was the adult condition at one time becomes an embryonic stage in future generations, and the series thus represents not only the ontogeny, but also, though in a more or less imperfect manner, the phylogeny of the organism.

The character of each stage in ontogeny must depend upon (1) the morphological and physiological constitution of the preceding stage, and (2) the nature of the environment in which development is taking place. We can not, however, distinguish sharply between those two sets of factors, for, in a certain sense, the environment gradually becomes incorporated in the organism itself as development proceeds, each part contributing to the environment of all the remainder, and the influence of this internal portion of the environment ever becoming more and more important.

The whole process of evolution depends upon changes of environment taking place so gradually that the necessary self-adjustment of the organism at every stage is possible. In the case of our amphibia the eggs could

possibly undergo the first stages of development, the preliminary segmentation, within the oviduct of the parent just as well as in the water, for in both cases they would be enclosed in their envelopes, and the morphological differences between the early stages in the two cases might be expected to be quite insignificant. But it must be the same at each term of the series, for each term is built upon the foundation of the preceding one, and the whole process takes place by slow and imperceptible degrees.

It is true that by the time we reach the formation of the vestigial gill-slits in the embryo of one of the higher vertebrates the environmental conditions are very different from those under which gill-slits were developed in their aquatic ancestors. But what then? Are not the gill-slits also very different? The changed environment has had its effect. The gills themselves are never developed, and the gill-slits never become functional; moreover, they disappear completely at later stages of development, when the conditions of life become still more different and their presence would be actually detrimental to their possessor. The embryo with the vestigial gill-slits is, as a whole, perfectly well adapted to its environment, though the gill-slits themselves have ceased to be adaptive characters. They still appear because the environmental conditions, and especially the internal conditions, which have now become far more important than the external ones, are still such as to cause them to do so.

I think the chief difficulty in forming a mental picture of the manner in which evolution has taken place, and especially in accounting for the phenomenon of recapitulation in ontogeny, which is merely another aspect of the same problem, arises from attempting to take in too much at once. There is no difficulty in understanding how any particular stage is related to the corresponding stage in the previous generation, and the whole series of stages, whether looked at from the ontogenetic or from

the phylogenetic point of view, can be nothing else but the sum of its successive terms.

It will be convenient, before going further, to sum up the results at which we have so far arrived from the point of view of the theory of heredity. We have as yet seen no reason to distinguish between somatogenic and blastogenic characters. All the characters of the adult animal are acquired during ontogeny as the result of the reaction of the organism to environmental stimuli, both internal and external. All that the organism actually inherits is a certain amount of protoplasm—endowed with a certain amount of energy—and a certain sequence of environmental conditions. In so far as these are identical in any two successive generations the final result must be identical also, the child must resemble the parent; in so far as they are different the child will differ from the parent, but the differences in environment can not be very great without preventing development altogether.

So far, it is clear, there has been no need to think of the germ-cells as the bearers of material factors or determinants that are responsible for the appearance of particular characters in the adult organism; nor yet to suppose that they are, to use the phraseology of the mnemonic theory of heredity, charged with the memories of past generations. They have been regarded as simple protoplasmic units, and the entire ontogeny has appeared as the necessary result of the reaction between the organism and its environment at each successive stage of development. This can not, however, be a complete explanation of ontogeny, for if it were we should expect all eggs, when allowed to develop under the same conditions from start to finish, to give rise to the same adult form, and this we know is not the case. We know also, from observation and experiment, that the egg is in reality by no means a simple thing but an extremely complex one, and that different parts of the egg may be definitely correlated with corresponding parts of the adult body. It

has been demonstrated in certain cases that the egg contains special organ-forming substances definitely located in the cytoplasm, and that if these are removed definite parts of the organism into which the egg develops will be missing. We know, also, that the nucleus of the germ-cell of either sex contains—at any rate, at certain periods—a number of perfectly well-defined bodies, the chromosomes, and these also have been definitely correlated in certain cases with special features of the adult organization.

Before we can hope to complete our mental picture of the manner in which organic evolution has taken place, if only in outline, it is evident that we must be able to account for the great complexity of structure which the germ-cells themselves have managed to acquire, and also to form some idea of the effect of this complication upon the development of both the individual and the race.

We must consider the origin of cytoplasmic and nuclear complications of the egg separately, for they appear to be due fundamentally to two totally distinct sets of factors. In the first place we have to remember that during oogenesis the egg-cell grows to a relatively large size by absorbing nutrient material from the body in which it is enclosed. It is this nutrient material that is used for building up the deutoplasm or food-yolk. There is good reason for believing that the character of this nutrient material will change, during the course of evolution, *pari passu* with the changing character of the organism by which it is supplied. Doubtless the change is of a chemical nature, for we know from precipitin experiments that the body fluids of closely allied species, or even of the two sexes of the same species, do exhibit distinctly recognizable differences in chemical composition. It also appears highly probable, if not certain, from such experiments as those of Agar upon *Simocephalus*, that substances taken in with the food, which bring about conspicuous modifications of bodily structure, may at the same time be absorbed and stored up by the egg-cells

so as to bring about corresponding changes in the adults into which the eggs develop.

There seems therefore to be no great difficulty in comprehending, at any rate in a general way, how the egg may become the repository of definite chemical substances, organ-forming substances if we like to call them so, possibly to be classed with the hormones and enzymes, which will influence the development in a particular manner as soon as the appropriate conditions arise.

Unfortunately, time will not allow of our following up this line of thought on the present occasion, but we may notice, before passing on, that with the accumulation of organ-forming substances in the egg we have introduced the possibility of changes in bodily structure, to whatever cause they may be due, being represented by correlated modifications in the germ-cells, and this is doubtless one of the reasons why the germ-cells of different animals are not all alike with regard to their potentialities of development.⁶

We now come to the question of how the nucleus of the germ-cell acquired its great complexity of structure. We are not concerned here with the origin of the differentiation into nucleus and cytoplasm and the respective parts played by the two in the life of the cell. The problem which we have to consider is the complication introduced by the sexual process, by the periodically recurring union of the germ-cells in pairs, or, as Weismann has termed it, amphimixis. This is well known to be essentially a nuclear phenomenon, in which the so-called chromatin substance is especially concerned, and it is a phenomenon which must have made its appearance at a very early stage of evolution, for it is exhibited in essentially the same manner alike in the higher plants and animals and in unicellular organisms.

Let us suppose, for the sake of argument, that when amphimixis first took place the chromatin of each germ-

⁶ Compare Cunningham's "Hormone Theory of Heredity" (*Archiv für Entwicklungsmechanik der Organismen*, Bd. XXVI, Heft 3).

cell was homogeneous, but that it differed slightly in different germ cells of the same species as a result of exposure to slightly different conditions during its past history. What would be likely to happen when two different samples of chromatin came together in the zygote? The result would surely depend upon the interaction of the complex colloidal multimolecules of which the chromatin is composed. Various possibilities would arise. (1) The two samples might differ in such a way as to act as poisons to one another, disturbing each other's molecular equilibrium to such an extent that neither could survive. This is possibly what happens when an ovum is fertilized by a spermatozoon of a distinct species, though there are, of course, exceptions. (2) They might be so alike as to be able to amalgamate more or less completely, so that there would simply be an increase of chromatin of possibly more or less modified constitution. (3) They might continue to exist side by side, each maintaining its own individual character.

In the third case the union of the two different samples would give rise to a mass of chromatin of twofold nature, and repetition of the process from generation to generation would, as Weismann has shown, result in ever-increasing heterogeneity, until the chromatin came to consist of a great number of different concrete particles, each of which might conceivably differ from all the others. But when two heterogeneous masses of chromatin meet in the zygote there may be all sorts of mutual attractions and repulsions between the different colloidal multimolecules, for all three of our supposed cases may arise simultaneously, and thus the results may become extremely complicated.

The chromatin of the germ-cells in all existing organisms is undoubtedly heterogeneous, and this heterogeneity may be to some extent visibly expressed in its arrangement in more or less multiform chromosomes during mitosis. We may provisionally accept Weismann's view that these chromosomes are themselves

heterogeneous, being composed of chromomeres or ids, which in their turn are composed of determinants.

All this complexity of structure may be attributed to the effects of oft-repeated amphimixis, a view which is supported in the most striking manner by the fact that the nucleus in all ordinary somatic cells (in animals and in the diploid generation of plants) has a double set of chromosomes, one derived from the male and the other from the female parent, and by the well-known phenomenon of chromatin reduction which always precedes amphimixis.

When we approach the problem of heredity from the experimental side we get very strong evidence of the existence in the germ-plasm of definite material substances associated with the inheritance of special characters. Mendelian workers generally speak of these substances as factors, but the conception of factors is evidently closely akin to that of Weismann's hypothetical determinants. The cytological evidence fits in very well with the view that the factors in question may be definite material particles and it is quite possible that such particles may have a specific chemical constitution to which their effects upon the developing organism are due.

From our point of view the interesting thing is the possibility that arises through the sexual process of the permutation and combination of different factors derived from different lines of descent. A germ-cell may receive additions to its collection of factors or be subject to subtractions therefrom, and in either case the resulting organism may be more or less conspicuously modified.

By applying the method of experimental hybridization a most fruitful and apparently inexhaustible field of research has been opened up in this direction, in the development of which no one has taken a more active part than the present President of the British Association. There can not be the slightest doubt that a vast number of characters are inherited in what is called the Mende-

ian manner, and, as they are capable of being separately inherited and interchanged with others by hybridization, we are justified in believing that they are separately represented in the germ-cells by special factors. Important as this result is, I believe that at the present time there exists a distinct danger of exaggerating its significance. The fact that many new and apparently permanent combinations of characters may arise through hybridization, and that the organisms thus produced have all the attributes of what we call distinct species, does not justify us in accepting the grotesque view—as it appears to me—that all species have arisen by crossing, or even the view that the organism is entirely built up of separately transmissible “unit characters.”

Bateson tells us that

Baur has for example crossed species so unlike as *Antirrhinum majus* and *molle*, forms differing from each other in almost every feature of organization.

Surely the latter part of this statement can not be correct, for after all *Antirrhinum majus* and *molle* are both snapdragons, and exhibit all the essential characters of snapdragons.

I think it is a most significant fact that the only characters which appear to be inherited in Mendelian fashion are comparatively trivial features of the organism which must have arisen during the last stages of phylogeny. This is necessarily the case, for any two organisms sufficiently nearly related to be capable of crossing are identical as regards the vast majority of their characters. It is only those few points in which they differ that remain to be experimented on. Moreover, the characters in question appear to be all non-adaptive, having no obvious relation to the environment and no particular value in the struggle for existence. They are clearly what Weismann calls blastogenic characters, originating in the germ-plasm, and are probably identical with the mutations of de Vries. These latter are apparently chro-

matin-determined characters, for, as Dr. Gates has recently shown in the case of *Oenothera*, mutation may result from abnormal distribution of the chromosomes in the reduction division.⁷

We have next to inquire whether or not the Mendelian results are really in any way inconsistent with the general theory of evolution outlined in the earlier part of this address. Here we are obviously face to face with the old dispute between epigenesis and preformation. The theory of ontogeny which I first put forward is clearly epigenetic in character, while the theory of unit characters, represented in the germ-cells by separate "factors," is scarcely less clearly a theory of preformation, and of course the conception of definite organ-forming substances in the cytoplasm falls under the same category. The point which I now wish to emphasize is that the ideas of epigenesis and preformation are not not inconsistent with one another, and that, as a matter of fact, ontogenetic development is of a dual nature, an epigenesis modified by what is essentially preformation.

We have already dealt briefly with the question of organ-forming substances in the cytoplasm, and it must, I think, be clear that the existence of these is in no way incompatible with a fundamental epigenesis. We shall find directly that the same is true of Mendelian "factors" or Weismannian "determinants."

We have seen that it is possible to conceive of even a complex organism as inheriting nothing from its parent but a minute speck of protoplasm, endowed with potential energy, and a sequence of suitable environments, the interaction between the two bringing about a similar result in each succeeding generation, with a slow progressive evolution due to the operation of the law of accumulation of surplus energy. If any of the conditions of development are changed the result, as manifested in the organization of the adult, must undergo a corresponding modification. Suppose that the chromatin sub-

⁷ *Quarterly Journal of Microscopical Science*, Vol. LIX, p. 557.

stance of the zygote is partially modified in molecular constitution, perhaps by the direct action of the environment, as appears to happen in the case of Tower's experiments on mutation in the potato beetle, or by the introduction of a different sample of chromatin from another individual by hybridization. What is the germ-plasm now going to do? When and how may the changes that have taken place in its constitution be expected to manifest themselves in the developing organism?

Let us consider what would be likely to happen in the first stages of ontogeny. If the germ-plasm had remained unaltered the zygote would have divided into blastomeres under the stimuli of the same conditions, both internal and external, as those under which the corresponding divisions took place in preceding generations. Is the presence of a number of new colloidal multimolecules in the germ-plasm going to prevent this? The answer to this question probably depends partly upon the proportion that the new multimolecules bear to the whole mass, and partly upon the nature of the modification that has taken place. If the existence of the new multimolecules is incompatible with the proper functional activity of the germ-plasm as a whole there is an end of the matter. The organism does not develop. If it is not incompatible we must suppose that the zygote begins its development as before, but that sooner or later the modification of the germ-plasm will manifest itself in the developing organism, in the first instance as a mutation. In cases of hybridization we may get a mixture in varying degrees of the distinguishing characters of the two parent forms, or we may get complete dominance of one form over the other in the hybrid generation, or we may even get some new form, the result depending on the mutual reactions of the different constituents of the germ-plasm.

The organism into which any zygote develops must be

a composite body deriving its blastogenic characters from different sources; but this cannot affect its fundamental structure, for the two parents must have been alike in all essential respects or they could not have interbred, and any important differences in the germ-plasm must be confined to the "factors" for the differentiating characters. The fundamental structure still develops epigenetically on the basis of an essentially similar germ-plasm and under essentially similar conditions as in the case of each of the two parents, and there is no reason to suppose that special "factors" have anything to do with it.

We thus see how new unit characters may be added by mutation and interchanged by hybridization while the fundamental constitution of the organism remains the same and the epigenetic course of development is not seriously affected. All characters that arise in this way must be regarded, from the point of view of the organism, as chance characters due to chance modifications of the germ-plasm, and they appear to have comparatively little influence upon the course of evolution.

One of the most remarkable features of organic evolution is that it results in the adaptation of the organism to its environment, and for this adaptation mutation and hybridization utterly fail to account. Of course the argument of natural selection is called in to get over this difficulty. Those organisms which happen to exhibit favorable mutations will survive and hand on their advantages to the next generation, and so on. It has frequently been pointed out that this is not sufficient. Mutations occur in all directions, and the chances of a favorable one arising are extremely remote. Something more is wanted, and this something, it appears to me, is to be found in the direct response of the organism to environmental stimuli at all stages of development, whereby individual adaptation is secured, and this individual adaptation must arise again and again in each succeeding

generation. Moreover, the adaptation must, as I pointed out before, tend to be progressive, for each successive generation builds upon a foundation of accumulated experience and has a better start than its predecessors.

Of course natural selection plays its part, as it must in all cases, even in the organic world, and I believe that in many cases—as, for example, in protective resemblance and mimicry—that part has been an extremely important one. But much more important than natural selection appears to me what Baldwin⁸ has termed “Functional Selection,” selection by the organism itself, out of a number of possible reactions, of just those that are required to meet any emergency. As Baldwin puts it, “It is the organism which secures from all its over-produced movements those which are adaptive and beneficial.” Natural selection is here replaced by intelligent selection, for I think we must agree with Jennings⁹ that we can not make a distinction between the higher and the lower organisms in this respect, and that all purposive reactions, or adjustments, are essentially intelligent.

Surely that much-abused philosopher, Lamarck, was not far from the truth when he said, “The production of a new organ in an animal body results from a new requirement which continues to make itself felt, and from a new movement which this requirement begets and maintains.”¹⁰ Is not this merely another way of saying that the individual makes adaptive responses to environmental stimuli? Where so many people fall foul of Lamarck is with regard to his belief in the inheritance of acquired characters. But in speaking of acquired characters Lamarck did not refer to such modifications as mutilations; he was obviously talking of the gradual self-adjustment of the organism to its environment.

⁸ “Development and Evolution” (New York, 1902), p. 87.

⁹ “Behavior of the Lower Organisms” (New York, 1906), pp. 334, 335.

¹⁰ “Histoire naturelle des Animaux sans Vertèbres,” Tom. I, 1815, p. 185.

We are told, of course, that such adjustments will only be preserved so long as the environmental stimuli by which they were originally called for continue to exercise their influence. Those who raise this objection are apt to forget that this is exactly what happens in evolution, and that the *sine qua non* of development is the proper maintenance of the appropriate environment, both internal and external. Natural selection sees to it that the proper conditions are maintained within very narrow limits.

A great deal of the confusion that has arisen with regard to the question of the inheritance of acquired characters is undoubtedly due to the quite unjustifiable limitation of the idea of "inheritance" to which we have accustomed ourselves. The inheritance of the environment is, as I have already said, just as important as the inheritance of the material foundation of the body, and whether or not a newly acquired character will be inherited must depend, usually at any rate, upon whether or not the conditions under which it arose are inherited. It is the fashion nowadays to attach very little importance to somatogenic characters in discussing the problem of evolution. The whole fundamental structure of the body must, however, according to the epigenetic view, be due to the gradual accumulation of characters that arise as the result of the reactions of the organism to its environment, and are therefore somatogenic, at any rate in the first instance, though there is reason to believe that some of them may find expression in the germ-cells in the formation of organ-forming substances, and possibly in other ways. Blastogenic characters which actually originate in the germ-cells appear to be of quite secondary importance.

We still have to consider the question, How is it that organic evolution has led to the formation of those more or less well-marked groups of organisms which we call species? We have to note in the first place that there

is no unanimity of opinion amongst biologists as to what a species is. Lamarck insisted that nature recognizes no such things as species, and a great many people at the present day are, I think, still of the same opinion. In practise, however, every naturalist knows that there are natural groups to which the vast majority of individuals can be assigned without any serious difficulty. Charles Darwin maintained that such groups arose, under the influence of natural selection, through gradual divergent evolution and the extinction of intermediate forms. To-day we are told by de Vries that species originate as mutations which propagate themselves without alteration for a longer or shorter period, and by Lotsy that species originate by crossing of more or less distinct forms, though this latter theory leaves quite unsolved the problem of where the original forms that crossed with one another came from.

I think a little reflection will convince us that the origin of species is a different problem from that of the cause of progressive evolution. We can scarcely doubt, however, that Darwin was right in attributing prime importance to divergent evolution and the disappearance of connecting links. It is obvious that this process must give rise to more or less sharply separated groups of individuals to which the term species may be applied, and that the differences between these species must be attributed ultimately to differences in the response of the organism to differing conditions of the environment. It may be urged that inasmuch as different species are often found living side by side under identical conditions the differences between them can not have arisen in this way, but we may be quite certain that if we knew enough of their past history we should find that their ancestors had not always lived under identical conditions.

The case of flightless birds on oceanic islands is particularly instructive in this connection. The only satisfactory way of explaining the existence of such birds is

by supposing that their ancestors had well-developed wings, by the aid of which they made their way to the islands from some continental area. The conditions of the new environment led to the gradual disuse and consequent degeneration of the wings until they either became useless for flight or, in the case of the moas, completely disappeared. It would be absurd to maintain that any of the existing flightless birds are specifically identical with the ancestral flying forms from which they are descended, and it would, it appears to me, be equally absurd to suppose that the flightless species arose by mutation or by crossing, the same result being produced over and over again on different islands and in different groups of birds. This is clearly a case where the environment has determined the direction of evolution.

In such cases there is not the slightest ground for believing that crossing has had anything whatever to do with the origin of the different groups to which the term species is applied; indeed, the study of island faunas in general indicates very clearly that the *prevention* of crossing, by isolation, has been one of the chief factors in the divergence of lines of descent and the consequent multiplication of species, and Romanes clearly showed that even within the same geographical area an identical result may be produced by mutual sterility, which is the cause, rather than the result, of specific distinction.

Species, then, may clearly arise by divergent evolution under changing conditions of the environment, and may become separated from one another by the extinction of intermediate forms. The environmental stimuli (including, of course, the body as part of its own environment) may, however, act in two different ways: (1) Upon the body itself, at any stage of its development, tending to cause adaptation by individual selection of the most appropriate response; and (2) upon the germ-plasm, causing mutations or sudden changes, sports, in

fact, which appear to have no direct relation whatever to the well-being of the organism in which they appear, but to be purely accidental. Such mutations are, of course, inherited, and, inasmuch as the great majority of specific characters appear to have no adaptive significance, it seems likely that mutation has had a great deal to do with the origin of species, though it may have had very little to do with progressive evolution.

Similarly with regard to hybridization, we know that vast numbers of distinct forms, that breed true, may be produced in this way, but they are simply due to recombinations of mutational characters in the process of amphimixis, and have very little bearing upon the problem of evolution. If we like to call the new groups of individuals that originate thus "species," well and good, but it only means that we give that name, as a matter of convenience, to any group of closely related individuals which are distinguished by recognizable characters from the individuals of all other groups, and which hand on those characters to their descendants so long as the conditions remain the same. This, perhaps, is what we should do, and just as we have learned to regard individuals as the temporary offspring of a continuous stream of germ-plasm, so we must regard species as the somewhat more permanent but nevertheless temporary offshoots of a continuous line of progressive evolution. Individuals are to species what the germ-plasm is to individuals. One species does not arise from another species, but from certain individuals in that species, and when all the individuals become so specialized as to lose their power of adaptation, then changes in the environment may result in the extinction of that line of descent.

It is scarcely necessary to point out that no explanation that we are able to give regarding the causes of either phylogenetic or ontogenetic evolution can be complete and exhaustive. Science can never hope to get to

the bottom of things in any department of knowledge; there is always something remaining beyond our reach. If we are asked why an organism chooses the most appropriate response to any particular stimulus, we may suggest that this is the response that relieves it from further stimulation, but we cannot say how it learns to choose that response at once in preference to all others. If we are asked to account for some particular mutation, we may say that it is due to some modification in the constitution or distribution of the chromosomes in the germ-cells, but even if we knew exactly what that modification was, and could express it in chemical terms, we could not really say why it produces its particular result and no other, any more than the chemist can say why the combination of two gases that he calls oxygen and hydrogen gives rise to a liquid that he calls water.

There is one group of ontogenetic phenomena in particular that seems to defy all attempts at mechanistic interpretation. I refer to the phenomena of restitution, the power which an organism possesses of restoring the normal condition of the body after it has been violently disturbed by some external agent. The fact that a newt is able to regenerate its limbs over and over again after they have been removed, or that an echinoderm blastula may be cut in half and each half give rise to a perfect larva, is one of the most surprising things in the domain of biological science. We can not, at present, at any rate, give any satisfactory mechanistic explanation of these facts, and to attribute them to the action of some hypothetical entelechy, after the manner of Professor Hans Driesch, is simply an admission of our inability to do so. We can only say that in the course of its evolution each organism acquires an individuality or wholeness of its own, and that one of the fundamental properties of living organisms is to maintain that individuality. They are able to do this in a variety of ways, and can sometimes even replace a lost

organ out of material quite different from that from which the organ in question is normally developed, as in the case of the regeneration of the lens of the eye from the iris in the newt. That there must be some mechanism involved in such cases is, of course, self-evident, and we know that that mechanism may sometimes go wrong and produce monstrous and unworkable results; but it is, I think, equally evident that the organism must possess some power of directing the course of events, so as generally to secure the appropriate result; and it is just this power of directing chemical and physical processes, and thus employing them in its own interests, that distinguishes a living organism from an inanimate object.

In conclusion I ought, perhaps, to apologize for the somewhat dogmatic tone of my remarks. I must ask you to believe, however, that this does not arise from any desire on my part to dogmatize, but merely from the necessity of compressing what I wished to say into a totally inadequate space. Many years of patient work are still needed before we can hope to solve, even approximately, the problem of organic evolution, but it seemed to me permissible, on the present occasion, to indulge in a general survey of the situation, and see how far it might be possible to reconcile conflicting views and bring together a number of ideas derived from many sources in one consistent theory.